Chapter 5

Monogamy and Infanticide in Complex Societies

Christopher Opie

Introduction

There has been a long history of attempts to explain the evolution of monogamy in mammals in general (Kleiman 1977), and primates in particular (Alexander 1979), partly because of the implications that it may have for the evolution of monogamy in humans. Monogamy is a complex term though, with some species invariably found in pairs (such as owl monkeys), whereas other species can be monogamous, but flexibly take up other mating systems (such as callitrichid monkeys). Humans fit with the latter flexible group, as well as having the additional distinction between their mating system and their marriage system. However, it is fairly well established that monogamy is common in birds (90% of species) (Lack 1968) due to the short time period between mating and egg laying that allows a male to increase his reproductive success through sharing high levels of offspring care (incubating, hatching and rearing), rather than leaving the female he has just mated with to look for other females with whom to mate. The particular reproductive strategy of mammals, with a long gestation period followed by lactation, reduces the opportunities for a male to provide direct care for his offspring, therefore most males move on after mating to seek other fertile females. As a result, monogamy is rare among mammals (5% of species) (Lukas and Clutton-Brock 2013). It is surprising, then, that monogamy is unusually prevalent in one particular mammal order, namely

the primates (where 30% of species are monogamous) (Opie, et al. 2013a), with monogamy occurring in all the major primate families (Opie, et al. 2012).

In mammals, the rare cases where monogamy has evolved have been suggested to result from unusual ranging behaviour of females in some species, which prevents males from pursuing a roving strategy. When females are spread out in the environment, where predation is low and resources are clumped (Emlen and Oring 1977; van Schaik and van Hooff 1983), or occupy small but discrete territories (Komers and Brotherton 1997), males are forced to stick with a single female or risk losing all their mating opportunities. Female behaviour of this sort may have been the trigger for a switch in mating strategy to monogamy in some mammal species, but this may not be the full explanation for the close pair-bonds found in primates and some other mammals (Kleiman 1977). For example, a small monogamous antelope species, klipspringer (*Oreotragus oreotragus*), which lives on rocky outcrops in sub-Saharan Africa, is found in monogamous pairs that occupy discrete territories, which they defend from conspecifics. However, Robin Dunbar (Dunbar and Dunbar 1974; Dunbar and Dunbar 1980) pointed out that the pair is much more closely bonded than would be necessary for the male simply to mate-guard the female, being rarely more than 10 meters apart and usually much less. At the same time, the male provides no direct care to their infant, suggesting that the pair's bonded behaviour is due to some indirect benefit that the male provides. Dunbar (1980) suggested that this indirect benefit was a predator detection role that allows the female to feed uninterrupted for long periods, but only if the pair maintains very close proximity and coordinated activity.

The male role in predator detection, as an explanation for monogamy in mammals, was initially also applied to primates (van Schaik and van Hooff 1983).

This explanation was first tested by Dunbar on large monogamous primates where the male provides no direct care for their infants (van Schaik and Dunbar 1990). Male gibbons (Hylobatidae), as well as providing no direct infant care, do not provide a predator detection role either. Furthermore, when a male's ability to monopolise more than one female at a time was tested, it was found that a gibbon male could patrol the territories of at least two females and probably up to five (van Schaik and Dunbar 1990), suggesting that males were choosing to form a pair rather that being forced into it by the ranging behaviour of the females. These results questioned the applicability of the general mammal explanation for the evolution of monogamy to primates and demanded a new hypothesis.

Van Schaik and Dunbar (1990) suggested that the evolution of monogamy in large primates could be explained as a response to the risk of infanticide by males, so ensuring that males stayed close to their infants even if they were not providing other paternal care or protection against predation. This new explanation for monogamy might also explain the characteristic 'duetting' in this primate family; it might function as a means of broadcasting the relationship status of the pair to any rival males that might be considering a takeover (van Schaik and Dunbar 1990). Indeed, it was later shown in long term gibbon (*Hylobates lar*) and siamang (*Symphalangus syndactylus*) studies that harm to infants by other males only occurred when the presumed father of the infant went missing or died (Borries, et al. 2011; Morino and Borries 2016).

Infanticide had previously been suggested as a driver of the evolution of primate mating systems more generally (Hrdy 1979). For example, Hrdy (1979) suggested that, in promiscuous primate species, conspicuous oestrous signals (female sexual swelling) induced multiple males to mate with a female, so confusing paternity

and reducing the risk of infanticide by those males. On the other hand, concealed ovulation (complete loss of oestrous signal) in a number of primate species was seen as a way of forcing males to stick close to a single female, eventually forming a monogamous pair, as the only reliable means of gathering information about that female's reproductive status. Monogamy then provided the males with guaranteed certainty of paternity, in turn ensuring that the males provided the infant care required for the highly dependent offspring of the pair (Alexander 1979; Turke 1984). In contrast, Hrdy and Whitten (Hrdy and Whitten 1987) argued that, rather than increasing paternity certainty, concealed ovulation also resulted in confusion as to which male had fathered the subsequent offspring. This was another way to protect infants from infanticidal males and induce tolerance from all the males that had mated with the infant's mother. One way to test these competing hypotheses is to examine the order in which the putative cause and effect traits appear or are lost over the course of primate evolution; a cause must always precede its effect. Sillen-Tullberg and Møller (1993) considered the order in which these traits were gained and lost during the course of primate evolution. Their analysis established that the oestrous signal was lost in promiscuous species, possibly for paternity confusion purposes, before the emergence of monogamy, suggesting that the loss of the oestrous signal may have influenced the evolution of monogamy itself (Sillen-Tullberg and Møller 1993).

Further support for a wide role for infanticide by males in driving primate mating systems was provided by a modelling study of the evolution of monogamy in small New World primates (callitrichids: Dunbar 1995a). Until this point, it had been fairly confidently assumed that the smaller primates, where males provided extensive paternal care, had evolved to become monogamous because of the need for these high

levels of male input (van Schaik and van Hooff 1983). Male marmosets for example, provide all infant carrying, grooming, and cleaning, leaving the female to focus solely on lactation. However, Dunbar (1995a) showed that despite male care having the reproductive benefits of enabling a female to have twins often, and to reduce the time interval between her broods, these changes could only have taken place after monogamy had already evolved. So, just as in the large monogamous primates, Dunbar proposed that male infanticide must have had an evolutionary role in the switch to monogamy (Dunbar 1995a).

Despite the fact that Dunbar's modelling studies strongly suggested a role for infanticide in the evolution of monogamy in primates, other researchers continued to argue that the standard model for the evolution of monogamy in mammals held for primates too (Brotherton and Komers 2003; Komers and Brotherton 1997). Komers and Brotherton (1997) used phylogenetic comparative methods across six mammal orders, including primates, to test the various explanations for the evolution of monogamy in mammals and argued that their study indicated that it was the ranging patterns of the females that caused mammal species to become monogamous. However, they questioned the role of large female territories and instead suggested that monogamy arose in those species where the females had small but exclusive territories that they actively defended from other females. The authors also confirmed that the male care of infants arose after the evolution of monogamy and not before, so that it was not implicated in the switch to this mating system. Komers and Brotherton (1997) concluded that primates show no differences from the general pattern for mammals, even though a much larger proportion of primate species were monogamous compared to mammals generally. The implication must be that many

primate species occupy habitats that allow females to have discrete territories, while other mammal species do not.

In effect, by the end of the 1990s, the primate monogamy debate had reached something of an impasse. While infanticide was at least implicated in the evolution of monogamy in a number of studies (Dunbar 1995a; Hrdy 1979; van Schaik and Dunbar 1990; Sillen-Tullberg and Møller 1993), other authors continued to argue that female ranging patterns were the key (Brotherton and Komers 2003; Komers and Brotherton 1997). The only progress that had been made was to rule out male care as a driver of monogamy in primates (Dunbar 1995a; Komers and Brotherton 1997). This led some researchers to propose that a combination of explanations may be plausible (Palombit 1999), while others doubted whether it would ever be possible to test between these hypotheses effectively because it is only possible to test the current function of monogamy and not its historical origin (van Schaik and Kappeler 2003).

Primate Sociality

At the same time, phylogenetic comparative methods were becoming increasingly common in evolutionary biology (Harvey and Pagel 1991). Using these methods it is possible to test evolutionary hypotheses by reconstructing the ancestral states for the traits of interest by analysing their evolution across a phylogenetic, or family, tree based on the genetic relationships between living species. It is also possible to determine whether a pair of traits changes together or independently of each other as they evolve across the tree, and crucially, which of them evolved first and therefore might be implicated in the evolution of the other.

While phylogenetic comparative methods have been used to investigate various aspects of primate social evolution, such as oestrous signal and mating

systems (Pagel and Meade 2006; Sillen-Tullberg and Møller 1993), there had been little focus on the evolution of primate social systems as a whole. However, a landmark paper (Di Fiore and Rendall 1994), using phylogenetic methods, showed that at least one group of primates, the baboons, retained the same social system despite living in very varied environments. These results questioned the theoretical underpinning of primate studies, the socioecological model (Sterck, et al. 1997), which argues that primate social systems are species' evolutionary responses to the habitat in which they live. It was therefore unclear whether primate social systems were a short-term response to ecological pressures as suggested by the socioecological model, or whether primates were constrained by their evolutionary history to stick with one system or with particular pathways between systems (Janson 2000).

Further improvements in phylogenetic methods (Pagel and Meade 2006) and the genetic data for building phylogenetic trees (Arnold, et al. 2010), on which these methods are based, meant that the time was right to try to resolve the impact of evolutionary history on primate social systems. Shultz et al. (Shultz, et al. 2011) used these methods to investigate the evolutionary pathways of primate social organisation and the constraint that evolutionary history may have played. They suggested that social organisation, at least, showed great inertia in primates, with very few changes across 75 million years of evolution. Secondly, their analyses revealed an unexpected model for the evolution of primate social organisation: instead of a steady progression from small and simple groups to large complex ones, or flexible changes between social states in response to environmental change, they found that the social organisation of primates moved directly from solitary individuals, foraging on their own and only coming together to mate, to large groups consisting of many adult

males and females with their offspring (see Figure 1). Only once this initial switch had taken place did switches into harem-based formations (a single male associated with multiple females) or pair living occur. Furthermore, in primates at least, there were no moves back to a solitary way of living once group living had been established.

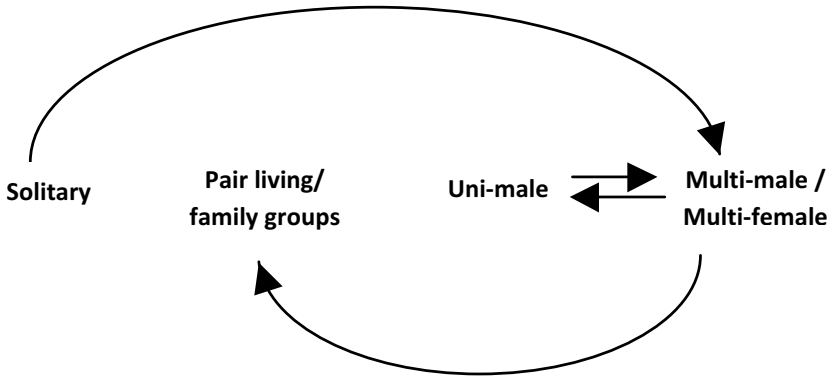

Figure 1. Evolution of social organisation in primates derived from RJ MCMC analysis (Shultz, et al. 2011). Arrows show the only transitions that are statistically significant across the model.

Perhaps the most interesting result, at least for this discussion, was that pair-living evolved directly from groups consisting of multiple adult males and females (claims to the contrary by Lukas and Clutton-Brock 2013 notwithstanding). This switch to monogamy came late in primate evolution (about 28 million years ago), based on the inferred age of the most recent common ancestor of living monogamous species. Furthermore, once monogamy had been established there were no further transitions out of this state (Shultz, et al. 2011). This suggests that monogamy is a cul-de-sac state from which, once adopted, there is no escape. The most likely reason for this is that the social bonds required to live in a monogamous pair are so demanding

that it needs major changes in brain organisation to support it that are difficult to undo (see also Chapter 11). Alternatively, it may be that there are other behavioural or physiological changes subsequent to the move to monogamy that makes the switch hard to reverse.

Primate Monogamy

Social systems consist of both social organisation (the way that animals live) and mating systems (the way that animals reproduce) (Kappeler and van Schaik 2002). For many primates, there is no difference between the way individuals live and the way they mate. However, for species that forage alone among the strepsirrhine family of primates, mating can vary between promiscuous (all the adult males mating with all the adult females in an area), polygynous (a single male monopolising mating with a number of females), and even monogamous. Furthermore, among some polygynous species of Old World monkeys (such as guenons and langurs), the single resident male can be swamped by an influx of out-group males at mating time, thereby switching the mating system from polygyny to something closer to promiscuity. A phylogenetic analysis of primate mating systems (Opie, et al. 2012) showed that from the ancestral state of promiscuous mating there were evolutionary switches to both polygynous and monogamous mating systems. Furthermore, there were also switches from polygynous to monogamous mating, but again, as with social organisation, once monogamy had evolved no species switched out of monogamy to an alternative mating system. This result demanded an investigation into the drivers for the evolution of monogamy to discover why so many primate species had evolved monogamy, and why it was such a stable state.

In order to establish which factors may be associated with the evolution of monogamy in primates and whether any of the hypotheses outlined above are supported, it is first necessary to establish whether the trait in question evolves in tandem with the mating system or independently of it. If the trait evolves together with the mating system, it is then possible to discover which trait switches first and which second. The timing of the switches then tells us whether the trait is likely to be a driver (or evolutionary cause) for the evolution of monogamy in primates, or whether the switch to monogamy prompted the evolutionary switch in the other trait. Predictions can be generated from each of the various hypotheses. Comparison between these predictions and what we actually observe during primate evolution then allows us to test between the different hypotheses for the evolution of monogamy in primates and determine which is the most likely (**Error! Reference source not found.**).

Table 1 Predictions for co-evolution between traits derived from the five hypotheses.

Hypothesis	**Predictions**
Paternal Care	Paternal care precedes monogamy
Female range size	Larger female ranges in monogamy
Discrete female ranges	Discrete female ranges precede monogamy
Concealed ovulation	Loss of oestrous signal precedes monogamy
Infanticide	Infanticide precedes monogamy

The phylogenetic analyses confirmed that primate mating systems evolved together with four of the traits in question: paternal care, discrete female ranges, concealed ovulation and male infanticide, but not with female range size. These

results were not surprising, since they support the previous research suggesting that these traits represent social behaviors that are closely linked with the evolution of monogamy. However, the demonstration that these traits evolve with monogamy does not tell us anything about causality. So let's consider each hypothesis in turn in the light of what these analyses tell us.

The original suggestion, particularly in small primates, was that male care for infants drove the evolution of primate monogamy (Kleiman 1977). The analyses showed that male care and mating systems evolved closely together across primate evolution, but monogamy was more likely to evolve from polygamous mating (in either promiscuous or polygynous form) in species that did not have paternal care compared to those species with male care (Opie, et al. 2013a). However, once monogamy evolved it was very likely that male care for infants would emerge, suggesting that the switch to monogamy facilitated the evolution of male care, and not the other way around. This result supports Dunbar's previous modeling work (Dunbar 1995a) and the phylogenetic studies (Komers and Brotherton 1997) which suggested that paternal care was a response to the evolution of monogamy rather than its cause. Furthermore, once male care had evolved in species that were already monogamous, there was no loss of male care – supporting the contention that this was a stable combination. In particular, once males got involved in providing care to their infants, females could respond by reducing the gap between births and in some cases producing twins, thereby making it less advantageous for the male to leave in order to pursue a roving male mating strategy (Dunbar 1995a). In effect, the male becomes locked into monogamy.

The second hypothesis for the evolution of monogamy across all mammals, including primates, was that large female range size forced a male to stick with a

female to have any chance of mating successfully (Lukas and Clutton-Brock 2013). However, the results showed, in line with a previous study (Komers and Brotherton 1997), that there was no association between mating systems and female range size (Opie 2013), suggesting that these two traits evolved separately across primate evolutionary history. Instead, again supporting a previous study (Komers and Brotherton 1997), the trait of females having discrete ranges and defending them from other females, evolved very closely with monogamy across primate evolution. However, contrary to the Komers and Brotherton (1997) study, monogamy was shown to be as likely to evolve with or without discrete female ranges, suggesting that it was not discrete ranges that caused the switch to monogamy. Furthermore, once monogamy had evolved, it was then far more likely for females to defend discrete ranges, suggesting that the switch to monogamy drove female ranging and not the other way around.

The third hypothesis was that monogamy arose in species where females had concealed ovulation. This was seen as a way to force a male to stick close to a female, eventually forming a monogamous pair, as the only means of gathering information about her reproductive state (Alexander 1979; Turke 1984). Opie (Opie 2013) found that mating systems did evolve together with concealed ovulation. The results also suggested that it was more likely for concealed ovulation to evolve in a polygamous mating system, while changes from polygamy to monogamy were far more likely to take place once concealed ovulation had arisen in females. This result supports the earlier study by Sillen-Tullberg and Møller (1993), which suggested that concealed ovulation in females evolved in promiscuous mating systems as a means of confusing paternity, possibly in response to infanticide, and that monogamy evolved after concealed ovulation evolved.

The final hypothesis for the emergence of monogamy was that it was a response to male infanticide, ensuring that both parents could protect their vulnerable infant. Opie et al. (Opie, et al. 2013a) showed that infanticide and mating systems evolved very closely together across primate evolution. Furthermore, monogamy only evolved from a polygamous mating system when infanticide was already present. Once monogamy had evolved, it was then very likely that infanticide would reduce, suggesting that the move to monogamy might be an effective counter-strategy to the infanticide threat.

This is such an interesting result that further investigation is warranted. It had been suggested that the risk of infanticide among non-seasonal breeders is determined by the ratio of lactation length to the length of gestation (van Schaik 2000; van Schaik and Kappeler 2003). For species where lactation is shorter than gestation, there is no problem for a female to conceive whilst nursing, because she will have finished nursing the first offspring by the time the second offspring is born. For species in which lactation is longer than gestation, however, a female would run the risk of having to nurse two infants of different ages simultaneously. In these species, females avoid such conflict by remaining infertile for some time during lactation, i.e. through lactational amenorrhoea. This, however, also increases the risk of infanticide by males, because by killing her infant a male can end the female's lactational amenorrhoea, thus making her available for mating sooner (van Schaik 2000). Monogamy may reduce infanticide risk by shortening the lactation period either though paternal care (Dunbar 1995a; Dunbar 1995b) or simply through the presence of a male who can protect the female and infant (van Schaik and Dunbar 1990).

We can test this hypothesis by asking whether monogamy reduced infanticide risk by shortening the weaning period. Analysis of the comparative data confirms that

lactation was significantly shorter compared to gestation in species with monogamy, particularly those species where the male provided infant care (Opie, et al. 2013a; Opie, et al. 2013b), supporting the suggestion that monogamy reduces the risk of infanticide by shortening the period when an unweaned infant is vulnerable. This result provides the remaining element in a compelling model of the evolution of monogamy in primates, and provides us with a simple unifying explanation as to why so many primate species are monogamous compared to mammals in general.

How Monogamy Might Have Evolved in the Primates

The findings outlined above suggest a sequence of events that looks something like the following.

The ancestor of all living primates lived about 75 million years ago (mya) (Arnold, et al. 2010), was a solitary forager (Shultz, et al. 2011) and mated promiscuously (Opie, et al. 2012). Group living evolved first among haplorhines (including the monkeys and apes) about 50 mya, although this did not happen in lemurs until much later (around 33 mya). However, as Dunbar and Shultz (2007) have pointed out, groups are complex places to live, and to help negotiate the social relationships that were crucial to an individual's reproductive success, brain sizes increased (see also Chapter 11). Large brains are energetically costly to grow, and many group-living primates solved this problem by increasing the duration of lactation so as to allow brain growth to continue over a longer period of time (Opie, et al. 2014a). Once lactation length had evolved to be longer than gestation length, females departed from the typical mammalian pattern (van Schaik 2000), and probable ancestral primate pattern, of mating during lactation. Instead, females in large-brained primate species had to delay their return to oestrus until they had

weaned their infant to avoid nursing two infants of different ages. However, by delaying her return to oestrus, a female rendered her unweaned infant vulnerable to infanticide by males who had not sired the infant (van Schaik 2000). Infanticide is very costly to females, so that a number of counterstrategies have evolved in primates, two of which involve the way females show that they are fertile (van Schaik 2000). First, conspicuous oestrous signals in females evolved in promiscuous mating systems (Pagel and Meade 2006), and are used to confuse paternity by ensuring that many males mate with the fertile female (Hrdy 1979) such that each then 'believes' himself to be the sire; this makes males more cautious about behaving infanticidally. Second, concealed ovulation in females may also have evolved to confuse paternity (Hrdy 1979; Sillen-Tullberg and Møller 1993), and could have preceded and contributed to the evolution of monogamy (Opie 2013) as a single male stayed close to a female so as to be able to monitor her reproductive state and be the first to mate with her when she returned to oestrus (Alexander 1979; Sillen-Tullberg and Møller 1993; Turke 1984). In any event, monogamy evolved only in those species that both faced significant infanticide risk *and* were more likely to have evolved concealed ovulation (Opie, et al. 2013a; Opie 2013).

Once monogamy had evolved in primate species, it was far more likely that high levels of male care evolved and that the monogamous pairs spread out in the environment (Opie, et al. 2013a). Both these features would have reduced infanticide risk, because male care for infants may have shortened lactation lengths due to a female being able to concentrate her efforts on lactation, relieved of other infant care (as happens in marmosets and tamarins: Dunbar 1995a). Occupying discrete ranges defended against other adults would have enabled the pair to monitor the activity of rival males and be better prepared to protect their offspring from them. A further

effect that reduced infanticide risk may have been a reduction in body and brain size in some monogamous primate species (Dunbar 2010; Montgomery, et al. 2010) that contributed to a reduction in the length of lactation needed to grow a large brain.

Great ape species have the largest brains of all primates (Dunbar and Shultz 2007). This means that lactation lengths are extremely long, up to 7 years among orang utans (Knott, et al. 2010), leaving infants vulnerable to infanticide for many years. Among gorillas, this extreme risk means that infanticide is the most likely cause of infant death despite considerable parental care (Harcourt and Greenberg 2001). Among our closest relatives, the chimpanzees and bonobos, promiscuity encouraged by conspicuous sexual swellings (Pagel and Meade 2006) ensures that paternity is confused and infants are relatively safe from attack by in-group males (van Schaik 2000). However, the lack of paternity certainty among *Pan* species means that male infant care is inevitably negligible; females provide all the parental care that infants receive until they are weaned.

This sequence of events raises the question as to how humans fit into the story. Humans and their hominin ancestors would have faced the same threats from infanticide as the other large-bodied, large-brained great apes. However, it seems that at some point on the lineage leading to modern humans since the most recent common ancestor with the two *Pan* species (about 6 mya), our ancestors evolved a form of pairbonded monogamy. We can't be certain when this happened, because none of the intermediate species have survived. However, there would seem to be two possibilities. One likely point is somewhere between the origin of the genus *Homo*, and the evolution of our species, *Homo sapiens*. Modelling work by Aiello and Key (Aiello and Key 2002) on the energetic requirements of *Homo erectus* suggest that, because of brain and body size increase with the evolution of this species, females

would have been unable to provision their infants by their own efforts alone; as a result, they would have needed to look to other adults, either female relatives and/or a male, for help. If so, then monogamy may have evolved at this point (Opie and Power 2008). Alternatively, it has been suggested that a predominantly monogamous mating system only evolved with the origin of *Homo sapiens*, with polygyny being characteristic of all preceding hominin species (Dunbar 2014; Nelson, et al. 2011).

There are good empirical grounds for thinking that monogamy is ancestral to hunter-gatherers, the original pre-agricultural state for humans (Chaudhary, et al. 2015; Walker, et al. 2011), although this evidence alone does not, of course, exclude the possibility that it evolved much earlier. However, humans are not obligate monogamists in the way that most monogamous primates are (the only exceptions are the New World callitrichid primates, whose social system is notoriously fluid and complex). Unlike the lifelong pairbonds of most monogamous primates, human pairbonds typically do not last more than a few years, unless socially enforced through formal marriage. Formal marriage probably arose with the advent of agriculture, because agriculture gave rise to property (land) that could be passed on to offspring (Hartung 1982). Passing property on to individuals who were not in fact one's genetic offspring would be a form of genetic altruism that would be heavily selected against by natural selection.

The accumulation of wealth in the form of land and livestock meant that rich men were able to afford more than one wife, and were able to pass on wealth to their sons who were then able to do the same (Hartung 1982). Polygynous marriage was probably the general pattern for early farming cultures as they expanded across the globe (Marlowe 2000; Opie, et al. 2014b; Opie 2013). Most cultures continue to allow polygyny to this day (Hartung 1982). However, a change took place among some

Indo-European cultures. Where land became fully utilised for agriculture, land-owning men were reluctant for their estates to be split between too many offspring and so resorted to monogamous marriage, although polygynous mating continued in the form of concubinage (Fortunato and Archetti 2010).

Conclusion

There is now a certain amount of clarity about the origins of monogamy in primates, including humans. For many years, some researchers have argued that primates fitted the general mammalian pattern with males of some species forced to stick with a single female because the ranging behaviour of those females precluded a male roving strategy. However, a number of primatologists have suggested that the much greater prevalence of monogamy in primates than in other mammals was due to the high risk of infanticide, in turn because large brained infants needed longer lactation periods. In this respect, Dunbar's work on the evolution of monogamy clearly ties up with his work on the social origins of primate brain evolution. In addition, using the latest phylogenetic techniques, it has now been possible to show that although monogamy evolved together with paternal care, discrete female ranges and infanticide, it was only infanticide that consistently preceded the switch to monogamy and could therefore be implicated in its evolution. As well as explaining why monogamy would be more prevalent in primates, infanticide holds the key to understanding the evolution of monogamy in humans. Large complex groups drove increased brain size in ancestral humans, which in turn exposed unweaned infants to extreme infanticide risk. Monogamy, within those large complex groups, was the human solution to ensure protection for infants from infanticidal males, which then allowed fathers to get involved in infant care. Although the majority of cultures

worldwide allow polygyny, most adults, even in these cultures, form monogamous pairs in order to raise their young. Even now we carry the evolutionary consequences of the way monogamy evolved across primate species; the breakdown in monogamous arrangements among humans, as with gibbons (Borries, et al. 2011), can still lead to increased harm and even death among young children (Daly and Wilson 1985; Hill and Kaplan 1988).

Acknowledgements

Christopher Opie is funded by a Leverhulme Early Career Fellowship.

References

Aiello LC, Key C. 2002. Energetic consequences of being a *Homo erectus* female. American Journal of Human Biology 14(5):551-565.

Alexander RD. 1979. Sexuality and sociality in humans and other primates. In: Katchadourian A, editor. Human Sexuality. Berkeley: University of California Press. p 81-97.

Arnold C, Matthews LJ, Nunn CL. 2010. The 10kTrees website: A new online resource for primate phylogeny. Evolutionary Anthropology 19(3):114-118.

Borries C, Savini T, Koenig A. 2011. Social monogamy and the threat of infanticide in larger mammals. Behavioral Ecology and Sociobiology 65(4):685-693.

Brotherton PNM, Komers PE. 2003. Mate guarding and the evolution of social monogamy in mammals. In: Reichard UH, Boesch C, editors. Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals. Cambridge: Cambridge University Press. p 42-58.

Chaudhary N, Salali GD, Thompson J, Dyble M, Page A, Smith D, Mace R, Migliano AB. 2015. Polygyny without wealth: popularity in gift games predicts polygyny in BaYaka Pygmies. Royal Society Open Science 2(5).

Daly M, Wilson M. 1985. Child abuse and other risks of not living with both parents. Ethology and Sociobiology 6(4):197-210.

Di Fiore A, Rendall D. 1994. Evolution of social organization: a reappraisal for primates by using phylogenetic methods. Proceedings of the National Academy of Sciences of the United States of America 91(21):9941-9945.

Dunbar R. 2014. Human evolution. London, New York: Penguin and Oxford University Press.

Dunbar RIM. 1995a. The mating system of callitrichid primates: I. conditions for the coevolution of pair bonding and twinning. Animal Behaviour 50(4):1057-1070.

Dunbar RIM. 1995b. The mating system of callitrichid primates: II. the impact of helpers. Animal Behaviour 50(4):1071-1089.

Dunbar RIM. 2010. Deacon's dilemma: the problem of pairbonding in human evolution. In: Dunbar RIM, Gamble C, Gowlett JAG, editors. Social Brain, Distributed Mind. Oxford: Oxford University Press. p 159-179.

Dunbar RIM, Dunbar EP. 1974. Social organization and ecology of the klipspringer (*Oreotragus oreotragus*) in Ethiopia. Zeitschrift für Tierpsychologie 35(5):481-93.

Dunbar RIM, Dunbar EP. 1980. The pairbond in klipspringer. Animal Behaviour 28(1):219-229.

Dunbar RIM, Shultz S. 2007. Evolution in the Social Brain. Science 317(5843):1344-1347.

Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197(4300):215-223.

Fortunato L, Archetti M. 2010. Evolution of monogamous marriage by maximization of inclusive fitness. Journal of Evolutionary Biology 23(1):149-156.

Harcourt AH, Greenberg J. 2001. Do gorilla females join males to avoid infanticide? A quantitative model. Animal Behaviour 62(5):905-915.

Hartung J. 1982. Polygyny and inheritance of wealth. Current Anthropology 23(1):1-11.
Harvey PH, Pagel MD. 1991. The Comparative Method in Evolutionary Biology. Oxford: Oxford University Press.
Hill K, Kaplan H. 1988. Tradeoffs in male and female reproductive strategies among the Ache: Part 1. In: Betzig L, Mulder MB, Turke P, editors. Human reproductive behaviour: A Darwinian perspective. Cambridge: CUP. p 291-305.
Hrdy SB. 1979. Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. Ethology and Sociobiology 1(1):13-40.
Hrdy SB, Whitten PL. 1987. Patterning of Sexual Activity. In: Smuts B, Cheney D, Seyfarth R, Wrangham R, Struhsaker T, editors. Primate Societies. Chicago: University of Chicago Press. p 370-384.
Janson CH. 2000. Primate socio-ecology: the end of a golden age. Evolutionary Anthropology 9(2):73-86.
Kappeler PM, van Schaik CP. 2002. Evolution of primate social systems. International Journal of Primatology 23(4):707-740.
Kleiman DG. 1977. Monogamy in mammals. The Quarterly Review of Biology 52(1):39-69.
Knott CD, Emery Thompson M, Stumpf RM, McIntyre MH. 2010. Female reproductive strategies in orangutans, evidence for female choice and counterstrategies to infanticide in a species with frequent sexual coercion. Proceedings of the Royal Society B: Biological Sciences 277(1678):105-113.
Komers PE, Brotherton PNM. 1997. Female space use is the best predictor of monogamy in mammals. Proceedings of the Royal Society B-Biological Sciences 264(1386):1261-1270.
Lack D. 1968. Ecological Adaptations for Breeding in Birds. London: Methuen & Co.
Lukas D, Clutton-Brock TH. 2013. The Evolution of Social Monogamy in Mammals. Science 341(6145):526-530.
Marlowe FW. 2000. Paternal investment and the human mating system. Behavioural Processes 51(1-3):45-61.
Montgomery S, Capellini I, Barton R, Mundy N. 2010. Reconstructing the ups and downs of primate brain evolution: implications for adaptive hypotheses and Homo floresiensis. BMC Biology 8(1):9.
Morino L, Borries C. 2016. Offspring loss after male change in wild siamangs: the importance of abrupt weaning and male care. Am J Phys Anthropol.
Nelson E, Rolian C, Cashmore L, Shultz S. 2011. Digit ratios predict polygyny in early apes, Ardipithecus, Neanderthals and early modern humans but not in Australopithecus. Proceedings of the Royal Society B: Biological Sciences 278(1711):1556-1563.
Opie C, Atkinson Q, Shultz S. 2012. The evolutionary history of primate mating systems. Communicative & Integrative Biology 5(5):1-4.
Opie C, Atkinson QD, Dunbar RIM, Shultz S. 2013a. Male infanticide leads to social monogamy in primates. Proceedings of the National Academy of Sciences 110(33):13328-13332.

Opie C, Atkinson QD, Dunbar RIM, Shultz S. 2013b. Reply to Dixson: Infanticide triggers primate monogamy. Proceedings of the National Academy of Sciences 110(51):E4938.
Opie C, Atkinson QD, Dunbar RIM, Shultz S. 2014a. Reply to Lukas and Clutton-Brock: Infanticide still drives primate monogamy. Proceedings of the National Academy of Sciences 111(17):E1675.
Opie C, Shultz S, Atkinson QD, Currie T, Mace R. 2014b. Phylogenetic reconstruction of Bantu kinship challenges Main Sequence Theory of human social evolution. Proceedings of the National Academy of Sciences 111(49):17414-17419.
Opie CF. 2013. The evolution of social systems in human and non-human primates. Oxford: University of Oxford.
Opie K, Power C. 2008. Grandmothering and female coalitions: a basis for matrilineal priority? In: Allen NJ, Callan H, Dunbar RIM, James W, editors. Early Human Kinship: From Sex to Social Reproduction. Oxford: Blackwell. p 168-186.
Pagel MD, Meade A. 2006. Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. American Naturalist 167(6):808-825.
Palombit RA. 1999. Infanticide and the evolution of pair bonds in nonhuman primates. Evolutionary Anthropology 7(4):117-129.
van Schaik CP. 2000. Infanticide by male primates: the sexual selection hypothesis revisited. In: van Schaik CP, Janson C, editors. Infanticide by Males and its Implications. Cambridge: Cambridge University Press. p 27–60.
van Schaik CP, Dunbar RIM. 1990. The evolution of monogamy in large primates: a new hypothesis and some crucial tests. Behaviour 115(1-2):30-61.
van Schaik CP, van Hooff JARAM. 1983. On the ultimate causes of primate social systems. Behaviour 85:91-117.
van Schaik CP, Kappeler PM. 2003. The evolution of social monogamy in primates. In: Reichard UH, Boesch C, editors. Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals. Cambridge: Cambridge University Press. p 59–80.
Shultz S, Opie C, Atkinson QD. 2011. Stepwise evolution of stable sociality in primates. Nature 479(7372):219-222.
Sillen-Tullberg B, Møller AP. 1993. The relationship between concealed ovulation and mating systems in anthropoid primates: a phylogenetic analysis. American Naturalist 141(1):1-25.
Sterck EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. Behavioral Ecology and Sociobiology 41(5):291-309.
Turke PW. 1984. Effects of ovulatory concealment and synchrony on protohominid mating systems and parental roles. Ethology and Sociobiology 5(1):33-44.
Walker RS, Hill KR, Flinn MV, Ellsworth RM. 2011. Evolutionary history of hunter-gatherer marriage practices. PLoS ONE 6(4):e19066.